

INTRASPECIFIC PREDATION IN *CLUBIONA CORTICALIS* (ARANEAE: CLUBIONIDAE)

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Clubiona corticalis is supposed to be a useful biological control agent of lepidopteran larvae (e.g. Tortricidae) in orchards. Thus, the levels of its intraspecific predation especially when bred in captivity must be determined. Predation is a risk at mating and dispersal. Cannibalism during mating, studied at 13°C, 20°C and 27°C and without prey in cages, remains low (1.5%) during the first 24 hours at all temperatures. After 24 hours cannibalism increased and was significantly higher at 27°C than at 13°C after one week. Males were 72% of the victims. Males can mate twice with different without increasing the risk of cannibalism. The spiders were studied for 12 days after dispersal. Until Day 3, no intraspecific predation occurred, whatever the availability of prey for juveniles. Intraspecific predation is very much reduced by the availability of sufficient prey, and a female given prey did not feed on its own progeny. *Clubiona corticalis* pourrait être utilisée en verger pour lutter contre des larves de lépidoptères (Tortricidae). Il était donc important de connaître les niveaux de prédation intraspécifique chez cette espèce, lorsqu'elle est élevée en captivité. Il est montré qu'il y a des risques de prédation à deux moments du développement: l'accouplement et la dispersion. Le cannibalisme durant l'accouplement, étudié à 13°C, 20°C et 27°C sans proie dans les enceintes, reste faible à toutes les températures (1.5%) pendant les premières 24 heures. Après 24 heures, le cannibalisme augmente. Il est significativement plus fort à 27°C qu'à 13°C après une semaine. Les mâles sont les victimes dans 72% des cas et peuvent s'accoupler deux fois avec des femelles différentes sans augmenter les risques de cannibalisme. Les jeunes araignées sont étudiées pendant douze jours après la dispersion. Quelle que soit la disponibilité en proies, aucun cas de prédation intraspécifique n'intervient jusqu'au troisième jour. Ensuite, la disponibilité en proies diminue de façon très significative le niveau de cannibalisme. A noter qu'une femelle disposant de proies, n'exerce aucune prédation sur sa progéniture. □Biology, Europe, laboratory, Araneae, France, breeding, auxiliary, intraspecific predation, *Clubiona corticalis*, dispersal, mating.

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Clubionids are wandering, nocturnal spiders (Marc, 1990a), and certain species are efficient in caterpillar control in orchards (Mansour *et al.*, 1980; Marc and Canard, 1989). The study of the arachnofauna in apple orchards led us to take an active interest in whether *Clubiona corticalis* (Walckenaer) can be used in biological control of pest caterpillars. In the laboratory, all instars of *C. corticalis* can consume large quantities of lepidopteran larvae, especially tortricids, harmful to orchards (Marc, unpublished data). However, the efficacy of using *C. corticalis* in biological control remains uncertain. Spiders are generally envisaged as having high rates of intraspecific and interspecific predation (Bristowe, 1958; Greenstone, 1978). If this is true for *C. corticalis*, then its effectiveness in biological control would be reduced, i.e., an increase in spider densities in the field would increase cannibalism. Thus, data on rates of cannibalism in *C. corticalis* are needed.

In *Anyphaena accentuata* (Walckenaer), *Philodromus cespitum* (Walckenaer) and *Diaea dorsata* (Fabricius) (the most abundant non-web spinning spiders in apple orchards), intraspecific and interspecific recognition minimizes cannibalism (Marc, 1992). Whether this is true of *C. corticalis* is not known. *C. corticalis* occurs in very high densities on pines (Marc, 1990b) where they build silk nests under bark for refuge during the day (Marc, 1990a). Partially flaking bark are favoured shelters on which concentrations of 6-12 nests can be found in 10-15cm² (often the clustered nests are stuck together). Furthermore, nests of other clubionids, *Clubiona brevipes* Blackwall, *C. leucaspis* Simon and *Ceto laticeps* (Canestrini), often adjoin those of *C. corticalis*. These aggregations suggest low intraspecific and interspecific predation in nature. However, laboratory bred spiders for use as auxiliaries may present special problems. In captivity, intraspecific predation at critical moments of develop-



ment may be artificially high because contact between individuals is more frequent. Mating and dispersal are likely to be critical periods (Fig. 1). This work determines levels of cannibalism in *C. corticalis* when bred in captivity.

MATERIALS AND METHODS

Subadult spiders (one instar before maturity) were collected in winter, in a forest under the bark of *Pinus sylvestris*. Removed from the field in Ependorff micro-tubes, they were separated into males (recognisable at this instar by a bulging palpal tarsus) and females. Each individual was then placed in Petri dishes (9 cm in diameter and 1.5 cm high) for breeding. Damp cotton wool kept humidity high in cages. Individuals were fed with two flies (*Lucilia*, Diptera) three times per week. Unless otherwise specified all procedures and observations were carried out in the laboratory. All enclosures are here referred to as 'cages'.

CANNIBALISM DURING MATING

In each of 135 Petri dishes, one male was placed with a virgin female, and no food was added for the week of the experiment. Breeding cages were kept at 13°C, 20°C and 27°C under long photoperiod (L:D=16:8), and were observed several times a day. Males and females used for mating had all moulted to adults at least two weeks before.

CANNIBALISM AFTER DISPERSAL

Dispersal, in this species, is when the juveniles at instar 2 leave the female's breeding-nest. Cannibalism, from dispersal (when the first juvenile leaves the breeding-nest) for 12 days was observed on eight egg masses from mating carried out. The egg masses were inside the female's cages (25ml Petri dishes). These observations were carried out at 20°C and in a L:D photoperiod of 16:8. Two groups of 4 egg masses each were set up:

- no prey for the juveniles. In two cages the female had been separated from her progeny.
- *Drosophila* provided for juveniles. The female was taken out of one dish.

Lucilia were given to the females left in the cages every day from the second day after the dispersal of the first of the juveniles. The caged spiders were observed 2-3 times a day for 12 days and the status—alive, death by cannibalism, or death by other causes, or still inside the nest—recorded.

RESULTS AND DISCUSSION

CANNIBALISM DURING MATING

In the final moult the reproductive organs are completely formed. Trophic, and locomotory activities and very different behaviour in two sexes of the *C. corticalis* species also appear (Marc, 1992). In the field, males become adults about 10 days before females (Marc, unpublished data). Males then seek females, inside whose nests mating takes place. Because of this asynchrony of maturity, males frequently mate with females soon after the latter moult and at which time females do not feed; they remain in their nest without feeding for 1-2 days after moulting (Marc, 1990a). These two days appear, therefore, to be an especially favourable time for the male to mate because, during this time, the female is only slightly aggressive. Males may also build a nest adjoining those of the subadult females and thus fertilise them soon after the final moult. This was also observed by Austin (1984) in *C. robusta* L. Koch and by Wolf (1990) in *Cheiracanthium pennyi* Cambridge and *Cheiracanthium punctorium* (Villers). The mating of many other species takes place just after the final moult of females. Jackson (1980a) reported that 161 species use tactics of cohabitation (the male stays with the immature female to mate with her after she has undergone her adult moult).

Here, successful mating could be obtained several weeks after the final moult of both sexes. The male approaches the female by tapping on her nest. Copulation, which takes place inside the female's nest, lasts for about 3 hours. The male, mounted on the female's back and facing the same direction, forms an angle of about 45° to her. From this position, he applies each palp consecutively into her epigyne. One male can fertilize the eggs of at least 3-4 females. Mating can also take place outside the female's nest without cannibalism. On the other hand, in other species, intraspecific interactions outside the nest were more 'lethal' (Jackson, 1988a; Jackson and Macnab, 1989).

Intraspecific predation was observed in 13% of the cases for all matings (Fig. 2). The most favourable conditions to reduce the risks of cannibalism during mating would have been to place the males in the female's cages just after the female's moulted, or, at least, in the presence of prey. Yet, here, males were brought to females which had moulted at least 15 days before. Furthermore, no food was provided. Because, to be practicable for production of auxiliary popula-

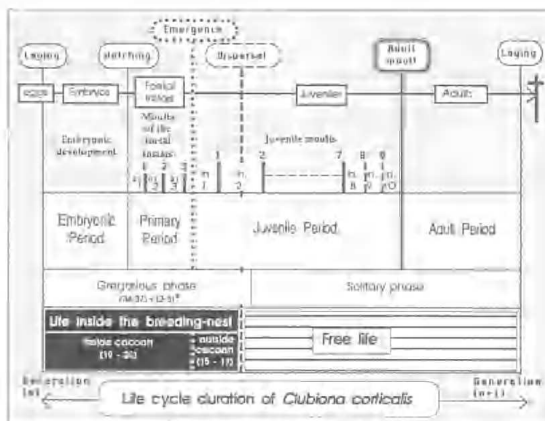


FIG. 1. Life cycle of *Clubiona corticalis*. Terminology in Canard (1987). *In. 1*, *in. 2* and *in. 3* indicate the foetal instars, and *in. 1* to *in. 10* the juvenile ones (last juvenile instars, 9 and 10, not present in every individual). Numbers in parentheses indicate duration in days. * (2-3) refer to Time spent by juveniles close to breeding-nest just after dispersal.

tions for biological control, the time needed for cure during laboratory breeding must be minimal. Synchronized mating was more practicable. Likewise, the absence of prey in the mating cages simplifies the work. Cannibalism observed after one week (13%) was very much higher than that in the field.

Predation before 24 hours, whatever the temperature, were rare (1.5%) (Fig. 2), but thereafter increased with time and after one week the rate of cannibalism was significantly lower (p) at a lower temperature (7.5% at 13°C and 18.5% at 27°C).

The spider's activity is probably related to the temperature. Indeed, locomotory activity increases with temperature and greatly increases the probability of interindividual encounters and, therefore, the risks of aggressiveness, especially in the absence of prey.

Cannibalism in 24 hours was rare, whatever the temperature, even though the trophic needs of females, especially after adult moulting, must be high considering ovule production. This can be explained simply by the smaller need for food after only one day of fasting, when this time is sufficient to guarantee mating. Indeed, the pairing time was quite short. Within 5 hours of the individuals being brought together, 75% of the matings had begun, and mating itself lasted 3 hours. We observed, however, that one male could mate several times with the same female which lengthens the interaction, but it seems that

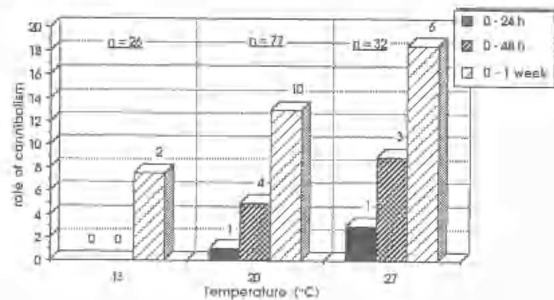


FIG. 2. Intraspecific predation rate during mating experiment on *C. corticalis* without prey at 13, 20 and 27°C. Symbols indicate the period of predation; n = no. of pairs tested; values on histogram bars = no. cases recorded.

this has no effect on the number of egg masses or on the descendants produced by the female. At 13°C no intraspecific predation occurred before 48 hours, and the females were fertilized normally and laid fertile eggs in the same way as at 20°C and 27°C.

In all pairs where intraspecific predation occurred once in the week after the start of the experiment, males are more often (72%) the victim. We did not observe a relation between weight and the individuals eaten, and sometimes smaller individuals ate larger ones. There is no significant sexual dimorphism in *C. corticalis*.

In contrast, even though size is not important, males do move more than females (Marc, 1990a). Conceivably, this weakens males relative to similar sized females. Furthermore, males who have smaller trophic needs and mate several times with different females display less aggressiveness towards their partners. This may partly explain why males were more often the victims of cannibalism.

A male can mate once or twice without significantly increasing the rate of cannibalism after one week (9% for one mating and 14% for two matings; $p > 0.05$). However, after two further matings (3 or 4), intraspecific predation increases significantly to 33% ($p < 0.05$) if compared to a male which mated only once. However, the male is not always the victim.

In *C. reichlini* Schenkel, males and females can mate several times without cannibalism (Hengmei and Hongquan, 1987). Equally, in interactions of *C. cambridgei* L. Koch, no cannibalism occurred between virgin males and females during the 38 interactions studied (Pollard and Jackson, 1982). Generally, species of *Clubiona* do not seem to be very aggressive

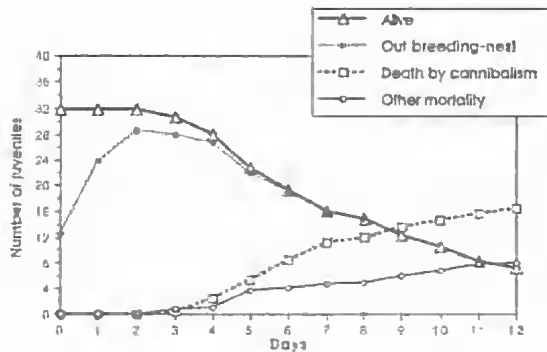


FIG. 3. Survival of juveniles (2nd instar) of *C. corticalis* during 12 days after dispersal, without prey.

toward each other during mating. Apparently, to eliminate cannibalism in *C. corticalis*, males and females should be brought together at about 13°C and individuals should be kept paired for about 24 hours. Furthermore, the presence of prey at 13°C should make the cohabitation of males and females perfectly feasible for several days without intraspecific predation occurring. Such conditions during mating should minimize the manpower needed and lower production costs.

CANNIBALISM AFTER DISPERSAL

Juveniles leave the breeding-nest, built by the female, after 1-4 days. Then, they remain grouped around the nest for about 2-3 days before dispersal. This gregarious phase lasts 17-20 days at 20°C (15-17 days in the breeding-nest and 2-3 days around the nest) (Fig. 1). It is only from the juvenile instar 2 (as defined by Canard, 1987), that juveniles begin to hunt. Until leaving the breeding-nest juveniles use on their vitelline reserves and, some attack the undeveloped eggs in the nest. Indeed, weight differences between juveniles leaving the breeding-nest indicate the existence of trophic activity in some individuals, as there are no significant weight differences known to occur between eggs in the same batch in the spider (Lecaillon, 1905). Furthermore, this trophic activity does not seem linked to the female feeding her juveniles by regurgitation or the consumption by the juveniles of a trophic egg-mass as, for example, in *Amaurobius* (Amaurobiidae) (Tahiri *et al.*, 1989). At this point, mortality is the highest in many species (Austin, 1984). It may be even more delicate in a captive breeding situation as the juveniles, in large numbers in the cages, would devour each other.

The dispersal of the juveniles given prey can

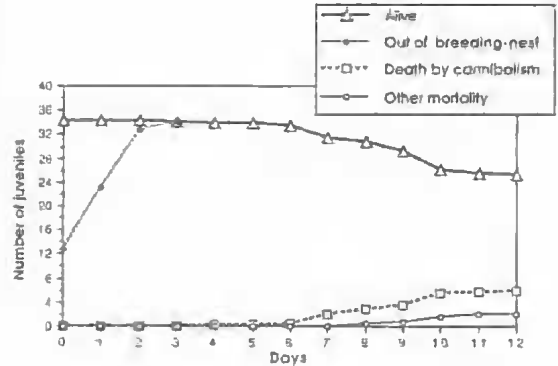


FIG. 4. Survival of juveniles (2nd instar) of *C. corticalis* in the presence of prey.

spread over 4 days (Fig. 3). There was no significant difference between the cages with a female and those with one removed ($p > 0.05$). Thus, females did not attack their own progeny after dispersal for at least the first 12 days and on the condition that prey was available. Cannibalism between the juveniles first began 3-4 days after the first dispersal and coincided with the expression of the first agonistic behaviour observed. Next, the number of juveniles decreased until there are about 10 individuals per cage towards the eleventh day.

When the juveniles were fed *Drosophila* (Fig. 4), the female's influence on this period of her progeny's development was similar. On the other hand, intraspecific predation was almost non-existent in the first 6 days and continued to be minimal afterwards, being about 5% after 10 days. There is a highly significant difference between the two groups after the 12 days of study ($p < 0.001$). Thus, with prey in the breeding cage, cannibalism decreased and was almost eliminated. Rypstra (1983), likewise, found in several spider species that intra-individual tolerance increased and cannibalism decreased when maintained at extremely high prey levels. Also, Krafft *et al.* (1986) were able to prolong the juvenile social period by giving juveniles abundant food. Austin (1984) recorded a high mortality in the breeding of *C. robusta*, cannibalism being one of the two major causes of mortality. On the other hand, in nature, spiders, which are potential prey of the highest density in the environment, only represented only 3% of prey actually consumed (Austin, 1984). Austin suggested that the highest mortality occurs at the dispersal instar.

The rest of the development presents fewer

Fam	Genus or species	Authority	
Club	<i>Supunna picta</i>	Jackson & Poulsen (1990)	
Gnap	<i>Taieria erebus</i>	Jarman & Jackson (1985)	
Liny	<i>Oedathorax insecticeps</i>	Kiritani <i>et al.</i> (1972)	
Lyco	<i>Lycosa pseudoannulata</i>	Kiritani <i>et al.</i> (1972)	
	<i>Pardosa lugubris</i>	Edgar (1969)	
	<i>P. purbeckensis</i>	Schaefer (1974)	
	<i>P. ramulosa</i>	Yeargan (1975)	
	<i>Pirata piraticus</i>	Schaefer (1974)	
	Mime	<i>Era aphana*</i> , <i>E. furcata*</i>	Gerhardt (1924), Bristowe (1941), Czajka (1963), Canard (1984)
	<i>Mimetus maculatus*</i> , <i>M. sp.*</i>	Jackson & Whitehouse (1986)	
Oxyo	<i>Peucetia viridans</i>	Turner (1979)	
Phol	<i>Halacnennus pluchei</i>	Blanke (1972)	
	<i>Phalculus phalangioides*</i>	Jackson & Brassington (1987), Jackson & Rowe (1987)	
Salt	<i>Brettus adanis**</i> , <i>B. cingulatus**</i>	Jackson & Hallas (1986a)	
	<i>Cacalus gibbasus</i>	Jackson (1990b)	
	<i>Cabanus mandibularis</i>	Jackson (1989)	
	<i>Cyryba algerina**</i>	Jackson & Hallas (1986a)	
	<i>C. acellata**</i>	Jackson (1990c)	
	<i>Euryattus sp.</i>	Jackson (1985a)	
	<i>Gelotia sp.**</i>	Jackson (1990d)	
	<i>Jacksanoides queenlandica°</i>	Jackson (1988a)	
	<i>Phaeacius malayensis</i> , <i>P. sp.</i>	Jackson & Hallas (1986a), Jackson (1990a)	
	<i>Plexippus paykulli</i>	Jackson & Macnab (1989)	
	<i>Phidippus jahnani</i>	Jackson (1977)	
	<i>Portia**</i>	Jackson & Hallas (1990)	
		<i>Partia fimbriata**</i>	Jackson (1982a, 1986b), Jackson & Blest (1982), Jackson & Hallas (1986b), Jackson & Wilcox (1990)
		<i>P. africana**</i> , <i>P. albimana**</i>	Jackson & Hallas (1986b)
		<i>P. labiata**</i> , <i>P. shultzi**</i>	Jackson & Hallas (1986b)
	<i>Simaeatha paetula</i>	Jackson (1985b)	
	<i>Tauala lepidus</i>	Jackson (1988b)	
Scyt	<i>Scytodes longipes</i>	Nentwig (1985)	
Ther	<i>Achaeareana camura</i>	Jackson (1988b)	
	<i>Achaeareana tepidiarum</i>	Rypstra (1986)	
	<i>Rhamphaeu</i>	Enders (1974)	

TABLE 1: Literature review of araneophagic spiders: species principally or strongly araneophagic. *, 'aggressive mimicry' = to perform a variety of vibratory behaviour in which the prey-spider responded as it normally would to its own prey. °, oophagy.

problems of cannibalism. Six groups of juveniles were bred together with 5 per Petri dish from instar 2-6 and no cannibalism was noted. Furthermore, the periodic absence of prey during a few

Family	Genus or species	Authority
Anyphaenidae	<i>Anyphaena accentuata</i>	Marc (1992)
Heteropodidae	<i>Olios diqna^k</i> , <i>O. lamarçki</i> , <i>O. abesulus</i>	Jackson (1987)
	<i>O. sp.</i>	
Hexathelidae	<i>Parrhathele antipadiana</i>	Jackson & Pollard (1990)
Philodromidae	<i>Philadramus cespitum</i>	Marc (1992)
Salticidae	<i>Halaplatys sp.</i>	Jackson & Harding (1982)
	<i>Myrmarachne lupata</i>	Jackson (1982b)
Thomisidae	<i>Diaea darsata</i>	Marc (1992)

TABLE 2: Literature review of araneophagic spiders: species which are little or not araneophagic. ^k, species kleptoparasitic which are not araneophagic.

days (3-5) in the cages did not result in intraspecific predation, but behaviour of escape and avoidance was observed. Similar observations had been made on sub-adults and adult females bred at 25-30 individuals per cage (30x20x20 cm) over 2 months.

Therefore, in breeding *C. corticalis*, the provision of *Drosophila* to juveniles at the dispersal stage should be sufficient to eliminate intraspecific predation. Then, 5 days after dispersal when all juveniles are out of the breeding-nest and no cannibalism has occurred, the division of these juveniles at instar 2 with about 5 per Petri dish, should prevent cannibalism later.

CONCLUSIONS

Intraspecific predation in *C. corticalis* during two especially susceptible periods of development (mating and dispersal) involves limited risks of cannibalism which can be eliminated. Mating must be at 13°C. Males in the enclosures with females must be limited to 24 hours, and dispersing juveniles must have sufficient prey. Cannibalism should not, therefore, be an obstacle to the mass breeding of this species for biological control.

Rates of intraspecific and interspecific predation have often been considered very high in spiders. The main enemies of spiders are often other spiders (Bristowe, 1941; Foelix, 1982). Certain species partially practice araneophagy (e.g. *Pardosa lugubris* (Walckenaer), *Lycosa annulata* Thorell), and a few make it their speciality (e.g. *Mimetus*, *Ero*, *Portia*) (Table 1). In fact, the species most studied for cannibalism are araneophagic in nature. In contrast, in other species, araneophagy appears to be almost non-existent (Table 2) even without prey (e.g. *Anyphaena accentuata*, *C. corticalis*, *Diaea dor-*

sata, *Philodromus cespitum*) and it is absent in social spiders such as *Mallos gregalis* (Simon) (Jackson, 1979, 1980). Behaviour of a few spider species cannot be applied to all. The degree of araneophagy of a species must be based on only that one. Therefore, the levels of intraspecific and interspecific predation amongst the more abundant species in agrosystems in which a spider is a possible biological control agent must be studied. A simple method has been finalised for spiders which do not spin a web (Marc, 1992).

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